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Original Article

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Most habitats are distributed heterogeneously in space, forcing animals to move according to both habitat characteristics and their needs for energy and safety. Animal space use should therefore vary according to habitat characteristics, a process known as the "functional response" in habitat selection. This response has often been tested vis-à-vis the proportion of a habitat category within areas available to individuals. Measuring sought-after resources in landscape where they are continuously distributed is a challenge and we posit here that both the mean availability of a resource and its spatial variation should be measured. Accordingly, we tested for a functional response in habitat selection according to these two descriptors of the resource available for a mountain herbivore. We hypothesized that selection should decrease with mean value of resources available and increase with its spatial variation. Based on GPS data from 50 chamois females and data on the actual foodscape (i.e., distribution of edible-only biomass in the landscape), we estimated individual selection ratio (during summer months) for biomass at the home range level, comparing edible biomass in individual home ranges and the mean and standard deviation of edible biomass in their available range. Chamois being a group-living species, available accessible ranges were shared by several individuals that formed socio-spatial groups (clusters) in the population. As expected, selection ratios increased with the standard deviation of edible resources in each cluster, but unlike our prediction, was unrelated to its mean. Selection of areas richer in resources hence did not fade away when more resources were available on average, a result that may be explained by the need for this capital breeder species to accumulate fat-reserve at a high rate during summer months. Low spatial variation could limit the selection of chamois, which highlights the importance of resource distribution in the process of habitat selection.

Key words: **chamois, foodscape, mountain ungulate, *Rupicapra rupicapra*.**

INTRODUCTION

Functional response in habitat selection (Mysterud and Ims 1998) is based on the idea that individuals pattern of habitat selection should vary with the relative availability of habitat types in the landscape (Holbrook et al. 2019), extending to the spatial dimension the well-known concept of functional response originally developed for understanding the rate of prey consumption by predators (Holling 1959). The relative availability of different habitats (Godvik et al. 2009) in an individual's range should indeed influence the time spent by an individual in each habitat, and consequently habitat selection processes (Charnov 1976; Brown 1988; Van Moorter et al. 2016). The understanding of how individual preferences change with the availability and characteristics of different habitats (i.e., the functional response in habitat selection) is essential to predict the impact of habitat changes on animal distribution at broader spatio-temporal scales (Aarts et al. 2008; Paton and Matthiopoulos 2016).

However, there are a number of hurdles to identifying functional responses in habitat selection (Beyer et al. 2010; Aarts et al. 2013). One is the choice of the predictor against which the response, in terms of habitat selection, is quantified. Studies of functional responses in habitat selection have initially relied on splitting available ranges in habitat categories of different suitability (e.g., empirical cases: Mysterud and Ims 1998; Godvik et al. 2009; Herfindal et al. 2009), mostly in terms of food resources and refuge in the context of the food/cover trade-off (Lima and Dill 1990; Mysterud and Østbye 1999). This approach is indeed particularly suited to

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contrasting habitat types such as closed versus open habitats, corresponding respectively to "safe and poor" and "risky and rich" combinations of risk and food resources in numerous species (Mysterud and Ims 1998; e.g., Dussault et al. 2005; Masse and Cote 2013). However, not all species live in such a categorical world: the distribution of food resources for instance may better be described by variables varying continuously in space. Yet, analyzing functional response in habitat selection with continuous resources remains challenging. As stated by Beyer et al. (2010), the "average magnitude of a continuous variable […] may not describe a functional response if the average magnitude is not a sufficient description of availability." Indeed, average values do not reflect the spatial variation of an actual habitat or resource (but see Gillies et al. 2006; Hebblewhite and Merrill 2008), while the extent of the spatial variation should constrain the selection: if a resource or habitat is distributed evenly, the potential for selection is nil. Although it has been neglected so far, we propose that the functional response in resource selection results both from the average value of a sought-after resource and its variability within the range available to an individual.

A second hurdle is that the shape of the response in terms of habitat selection is expected to be nonlinear (Holling 1959 in the context of predator prey functional response; Aarts et al. 2008 in the context of habitat selection), which means the detection of a functional response or lack thereof may depend on the range of values of the resource variables against which the response is tested. Indeed, even a preferred resource may not be selected for if rare and hard to detect or get to. Likewise, as mentioned above, no selection should be detected if a preferred resource is very abundant and uniformly distributed in space within an individual's available range. Hence, the larger the contrast in resources in available ranges among individuals, and the higher the spatial variation in resource availability, the more likely it is to detect a functional response in habitat selection (Holbrook et al. 2019). Testing for functional response in habitat selection therefore requires awareness of potential nonlinearity in the functional response vis-à-vis both the mean value and spatial variation of the sought-after resource.

Given that seeking a functional response in habitat selection relies on comparing habitat selection among individuals whose habitat availability differs, a third pivotal question is the identification and delimitation of the area available for each individual. This step is crucial as all metrics of habitat selection (Lele et al. 2013; Holbrook et al. 2019 for reviews) are contingent upon the delimitation of the available area (Johnson 1980), a fact that is not always recognized and therefore often overlooked (Beyer et al. 2010). Likewise, selection is assumed to be a consequence of a selection process occurring within an available range which is accessible and known to the animal (Aarts et al. 2008; Beyer et al. 2010), although getting information about accessibility and animal cognitive map (Fagan et al. 2013) outside its home range is a difficult task (Gaillard et al. 2010). Here, we will approach this question explicitly (though indirectly), by considering the accessible available range of an individual to be the assembled range used by the conspecific it overlaps most of the time with (i.e., the group of individuals it shares space with). Our solution relies on studying a group-living species, which has seldom been done so far in the context of studies of functional response in habitat selection. Indeed, it has first been studied in territorial species (e.g., roe deer, Mysterud and Ims 1998; Pellerin et al. 2010) with nonoverlapping individuals. By focusing on a group-living species here, we should get a definition of the available range for each individual, which accounts for its accessibility, an implicit assumption which is rarely dealt with in the habitat selection literature (Beyer et al. 2010; Pellerin et al. 2010; Bastille-Rousseau et al. 2015; Panzacchi et al. 2016)

Our study species for looking at the functional response in habitat selection is the chamois (*Rupicapra rupicapra*), a medium-sized herbivore (Crampe et al. 2007; Loison et al. 2008) living in mountainous systems characterized by high spatial variation of habitat at fine scale (Duparc et al. 2012). As mentioned above, it is a group-living species, and several individuals could share a common area, in which they can encounter a large spatial variation of the food resource availability. This species is so a particularly relevant model to seek for a functional response vis-à-vis a continuously distributed resource variable, which can be characterized by both a mean value and a spatial variation. We leveraged a unique combination of three large data sets on habitat characteristics (distribution, composition, and biomass of plant communities) defined through remote sensing and field sampling (Duparc et al. 2012; Duparc 2016), individual habitat use obtained by GPS collars (Tablado et al. 2016), and diet, determined using DNA barcoding (Bison 2015; Thuiller et al. 2017). More specifically, we determined the shape of the functional response by comparing habitat selection patterns among individuals from several subpopulation units monitored throughout the growing season. We characterized habitats within the available range of each chamois using the biomass of edible plants as a proxy of the availability of food resources. Focusing on the biomass of the subset of plants that are edible for chamois and not on the overall biomass allowed us to describe the actual foodscape, as seen through the eyes of the consumer (Searle et al. 2007). Our analyses followed three steps. First, using the GPS database, we determined subpopulation spatial units (hereafter "clusters") based on a clustering algorithm applied on individual home range overlaps. Each individual was hence attributed to one cluster. We considered that a cluster range was available and accessible for all the individuals assigned to this cluster. Second, combining the diet database and the habitat database, we estimated, for each month, the edible biomass and the spatial variation in edible biomass both at cluster and individual home range levels. Third, we estimated habitat selection patterns of each individual by comparing edible biomass within individual monthly home ranges to edible biomass within an individual's cluster range. We tested whether habitat selection for edible biomass differed among clusters, i.e. whether chamois of the same subpopulation unit have similar selection behavior in response to similar habitat characteristics (H1). Then we tested whether habitat selection was driven by availability described in terms of mean and spatial variation of edible biomass within each cluster. On the one side, we expected (H2) a decrease in the selection with an increasing mean of edible biomass in cluster range if there is a saturation effect (Holling 1959; Mysterud and Ims 1998): if edible biomass becomes nonlimiting in an individual available range, there would be no incentive for an individual to use its available range selectively. On the other side, we expected (H3) an increase in selection according to the spatial variation of edible biomass, starting with a lack of selection in case biomass, whatever its mean value, is distributed homogeneously in the available range.

MATERIALS AND METHODS

Study area

We conducted our study in the National Game and Wildlife Reserve of Les Bauges massif, in the northern French Alps (45°40′ N, 6°14′ E; 900 to 2200 m a.s.l., 5200 ha). More than half of the

area (56%) is covered by forests dominated by beech (*Fagus sylvatica*) and fir (*Abies alba*) groves. Thirty-six percent is grassland and the remainder rocky areas (Lopez 2001). The alpine pastures, where chamois mostly reside in summer, were composed of seven plant communities, based on dominant species: alpenrose heaths, Blue moor grass–evergreen sedge swards, matgrass swards, mountain hay meadows, rusty sedge grasslands, tall herb community, and screes (details in Duparc et al. 2012). The "scree" category grouped all plant associations found on steep slopes and habitat dominated by boulders and fallen rocks. No noticeable changes in landcover occurred during the 10 years of the study period (2004–2013, from our own expertise based on intensive field work during summer months).

Chamois population survey

Chamois is a medium-sized dimorphic ungulate (average body mass of 30 kg for females and 40 kg for males, Garel et al. 2009). Chamois females reproduce for the first time at 2 or 3 years of age. They give birth to one young per year in late May (Loison 1995) and form groups with other females, kids and yearlings (Boschi and Nievergelt 2003; Crampe et al. 2007). Chamois is a gregarious species with a clan-like organization, that is, with groups that can be quite loose (Gerard and Richard-Hansen 1992; Boschi and Nievergelt 2003; Crampe et al. 2007), but with adult females keeping to the same home ranges from year to year (Loison et al. 1999; Loison et al. 2008). In our populations, female chamois lived in groups of 19 ± 18 individuals on average (mean ± SD, quantile 5% = 1, quantile 95% = 56, values calculated with 925 observations on 172 marked females during summer between 2008 and 2018). We focused on the growing season (June–August) following the birth peak (Loison 1995), when nursery groups composed of young, reproductive and nonreproductive females are formed (Gerard and Richard-Hansen 1992; Ruckstuhl and Ingold 1999). This period is highly critical for mountain ungulates (Pettorelli et al. 2007; Hamel et al. 2009) due to the high-energy requirements for lactation and storage of fat reserves for winter survival (Clutton-Brock et al. 1989; Jönsson 1997). Chamois have no natural large predators in the study area, except for golden eagles (*Aquila chrysaetos*) and red foxes (*Vulpes vulpes*) that may occasionally predate on newborns and sick individuals. During the study period, chamois population density remained quite stable, as attested by the low interannual variation in kid body mass (unpublished data, Mathieu Garel).

We trapped 50 female chamois during spring-summer 2004–2013 using falling nets baited with salt licks. These were located in two alpine grassland sites (Trelod: n = 29 captures; Pecloz: n = 21 captures) 9.9 km apart without exchanges of chamois females between areas (Loison et al. 2008). Animals were fitted with Lotek 3300S GPS collars (Engineering Inc.), which recorded one location per day (over the different schedules used during the study period). We screened GPS data for positional outliers (n = 262; 1.21% of the full data set) based on unlikely movement characteristics (Δ = 5 000, μ = 4 000, α = 90% quantile of movement speed from a focal individual, θ = −0.90, Bjørneraas et al. 2010).

Home range estimate

We estimated monthly home ranges and annual home ranges used by each individual from a utilization distribution (UD) computed using the Brownian bridge movement model (BBMM; Horne et al. 2007). BBMM is a continuous-time stochastic model of movement that incorporates an animal's movement path and time between locations to calculate UD, the probability density function providing the likelihood of an animal occurring in each unit of a defined area. The locations recorded by immobile GPS collars in the field (number of collars = 6; number of locations = 4343) were used to compute GPS location error (15 m here) from BBMM as the median distance between the centroids of data recorded by a GPS collar and each of these locations. The Brownian motion variance was determined for each monthly trajectory using the maximum likelihood approach developed by Horne et al. (2007). We thus defined home ranges as the set of pixels of a 25 m × 25 m grid including 90% of the space use estimated by BBMM, to avoid the inclusion of unused areas (Bjørneraas et al. 2012). Fifty-nine annual home ranges (as nine animals were surveyed 2 years) were estimated for the clustering and 212 monthly home ranges (June = 60, July = 64, August = 88) were used in the habitat selection analyses.

Statistical analyses

Defining accessible available area for each individual

We strived to delimit the available accessible area (see Introduction) for each individual. We accounted for the clan-like organization of chamois by clustering individuals whose annual home ranges strongly overlapped, and considered that the combined area used by all individuals of a cluster could be considered as accessible and known for any individual in this cluster. Chamois living on average for ca. 8 years, and up to 20 years (Loison et al. 1999; Bleu et al. 2015), it likely knows a larger area than what it covers during each summer month. Spatial clusters were identified using hierarchical clustering (Sneath 1957) on a matrix of Jaccard distances computed from the spatial overlap between annual home ranges of each pair of individuals (see details in Supplementary Appendix S1). We chose a number of clusters that included at least three individuals in each cluster and had the largest scores of the average silhouette width (Rousseeuw 1987; Borcard et al. 2011). The available area associated to each individual corresponded to the union of all the summer month home ranges of individuals belonging to its cluster.

Estimating resource availability

Second, we estimated the quantity of edible biomass (foodscape) at the level of 25 m × 25 m pixels in each cluster (Duparc et al. 2012). We modeled biomass during the whole study period (2003–2014), combining field data (plant composition and green biomass), diet data (Rayé et al. 2011; DNA barcoding of feces, Bison et al. 2015), and remote sensing (NDVI, see details in Supplementary Appendix S2). We could therefore predict weekly values of biomass of edible plants at the 25 m × 25 m scale for the whole study area and for the whole study period. Then from these values, we estimated the mean and spatial variation (the standard deviation of biomass value per pixel, SD) of biomass of edible plants in each cluster every month and every year (n = 86 cluster-month-year). Finally, we computed the mean edible biomass within the monthly home range of each chamois (n = 212 chamois-month-year, Duparc et al. 2019).

Patterns of resource selection and functional response

To estimate selection, we calculated year- and month-specific selection ratios w (Savage 1931; Manly et al. 2002; Lele et al. 2013) for edible biomass for each chamois. As recommended by Holbrook (2019), we chose selection ratio because it is the most suited metric to investigate understanding of functional response and because it is independent of individual-level intercepts. We calculated selection ratio for the i^{th} individual (n = 212) as: $w_i = o_i/\pi_i$, where "π"

and "o" represent average values of edible biomass in the cluster and in the 90% home range of the individual, respectively (see "home range estimate" section for details). To assess whether selection differed among clusters, we used mixed-effect models of selection ratios for edible biomass, where cluster was a fixed effect, and year, month (nested in year) and individual were random effects (Bates et al. 2015, package "lme4" in R). We tested for the cluster effect by performing the Likelihood Ratio Test (LRT) comparing full model to null model. Finally, we considered 95% confidence intervals that did not overlap with 1 (no selection) as indicating a significant selection for (if $w_i > 1$) or against (if $w_i < 1$) the focal variable.

We then investigated for a functional response in selection for edible biomass according to edible biomass mean and SD values in cluster ranges. We tested separately the effect of mean and SD of biomass as explanatory variable because they were correlated ($r = 0.52$). In addition, we tested for the relationship between selection ratios and residual variation of biomass (retrieved using a linear model: biomass~SD). By doing so, we answered whether selection ratios decrease, controlling for spatial variation, when biomass increases, due to a fading incentive for individuals to be selective. Likewise, we tested for the relationship between selection ratios and the residual variation of SD (model: SD~biomass), and answered whether, controlling for biomass, selection ratios increase with spatial variation. As we expected nonlinear functional responses (Aarts et al. 2008), we used general additive mixed model (Wood and Scheipl 2017, package "gamm4" in R) with selection ratios as the response variable and either explanatory variables (biomass, SD, residuals of the biomass vs. SD linear relationship, and residuals of the SD vs. biomass linear relationship) in the model (smoothing parameter), while year, month (nested in year), cluster and individual (nested in cluster) were random effects (Bates et al. 2015, package "lme4" in R). We considered individuals to behave independently one to another, even in the same cluster, as our GPS-marking pressure was low every year (50 females in 10 years in a study site comprising 6 clusters), resulting in the likelihood of individuals belonging to the same (loose; see "Chamois population survey" section) group to be low. We also tested for the effect of each variable by performing the Likelihood Ratio Test (LRT) comparing full model to null model, and we considered 95% confidence intervals that did not overlap with 1 (no selection) as indicating a significant selection for (if $w_i > 1$) or against (if $w_i < 1$) the focal variable.

We estimated the proportion of variance explained by each variable by computing the marginal R^2 and conditional R^2 in the footsteps of Nakagawa and Schielzeth (2013). Marginal R^2 is concerned with variance explained by fixed factors, and conditional R^2 is concerned with variance explained by all parts of the model (both fixed and random factors).

RESULTS

Defining and comparing availability among clusters

Clustering on annual home ranges provided support for six clusters (Figure 1, Supplementary Appendix S1). The number of individuals per cluster varied from 3 to 18 and the number of individual-month-year (on which selection ratios were estimated) per cluster were 9, 17, 49, 30, 72, and 35 for clusters 1 to 6, respectively (see Figure 1 for cluster number and position in the study site). The average individual monthly home range size was 66 ha (95% confidence interval [CI]: 60–72), while cluster surface areas varied from 150 to 511 ha. Areas and number of individuals per clusters were not correlated (Pearson correlation test: $t = 1.08$, df = 4, $P = 0.34$, $r = 0.47$).

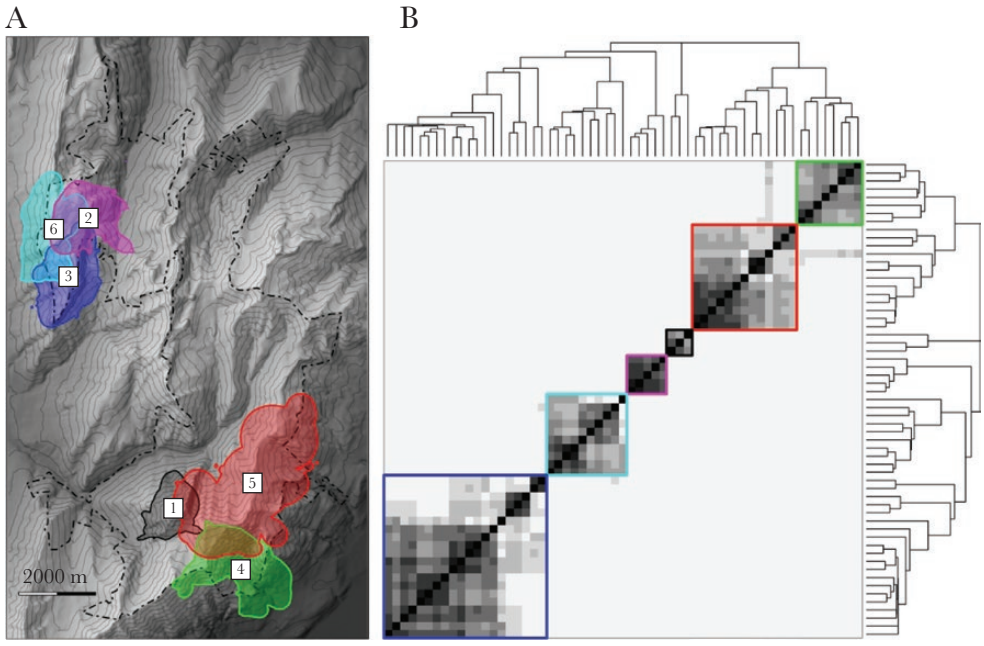

Figure 1
Hierarchical clustering: (a) Location of the six clusters in the National Game and Wildlife Reserve of Les Bauges massif (dot-dash line). (b) heat-map of matrix of Jaccard distance calculated on annual home range overlap for every pair of chamois (white: Jaccard distance = 1 to black Jaccard distance=0). Dendrograms on right and top sides were obtained by hierarchical clustering using "single link" method. Colors of squares correspond to cluster colors on the map (a).

During the study period mean Jaccard indices by cluster calculated on summer home ranges ranged from 0.37 to 0.50, cluster 3 excepted (Jaccard index = 0.29, Figure 2). This means that between a third and a half of the home range sums of all individuals' pairs were shared while individuals of different clusters did not share any area (Jaccard indices close to 0). This supports that clusters were well discriminated.

Clusters were contrasted in terms of topography and proportions of plant communities (Supplementary Appendix S1). Proportions of northern and southern aspect classes varied from 3.5% to 32.6% and from 15.2% to 50.6%, respectively. Intermediate slopes ([30°; 45°]) covered approximately half of clusters (mean = 52.9 ± 6.7%), whereas steep slopes ranged from 13.0% to 32.4%. The area within spatial clusters was covered with forests (dominated by beech and spruce; from 12.7% to 57.8%), swards (dominated by *Sambucus caerulea*; from 19.5% to 56.6%), rocky areas (from 4.8% to 17.0%), meadows (from 0.0% to 17.6%) and minor amounts of other plant communities (riparian forests, shrub lands, heaths and other grassland types). These differences among clusters in their composition of plant communities resulted in marked differences in mean and spatial SD of available edible biomass. Mean edible biomass ranged from 17.1 ± 1.6 g/m^2 for cluster 4 to 25.6 ± 1.2 g/m^2 for cluster 2 and SD of edible biomass ranged from 14.6 ± 1.3 g/m^2 for cluster 4 to 30.9 ± 0.97 g/m^2 for cluster 6 (Figure 3). Both variables were correlated (t = 8.709, df = 210, P < 0.001, r = 0.52 [95% CI 0.41–0.61], Figure 4a).

Influence of local forage resource availability on habitat selection

The selection of edible biomass varied among clusters (LRT: df = 5, Chi^2 = 42.9, P < 0.001) in agreement with H1. Selection ratios ranged from 0.97 ± 0.04 (not different from 1, i.e., no selection) for cluster 5 to 1.52 ± 0.06 (over selection of areas with more edible biomass) for cluster 4 (Figure 4b). However, contrary to our hypothesis that selection should fade away with increasing biomass (H2), selection ratios were related neither to the mean edible biomass (LRT: df = 2, Chi^2 = 4.01, P = 0.13) nor to the residuals of the mean biomass in clusters (i.e., accounting for SD, LRT: df = 2, Chi^2 = 1.98, P = 0.37). Chamois selected for areas with higher mean biomass whatever the available mean biomass, whether spatial SD is controlled for or not (average selection ratio of 1.16 ± 0.08 estimated over all individual-month-year, Figure 4c with mean biomass, Supplementary Appendix 3 for residual biomass).

In agreement with our hypothesis that selection should increase with the spatial variation of edible biomass in the available range (H3), the larger the values of spatial SD, the more chamois were selective (absolute values of SD: LRT: df = 2, Chi^2 = 11.22, P = 0.004; residuals of SD accounting for biomass: LRT: df = 2, Chi^2 = 9.55, P = 0.008). The shape of the functional response was nonlinear (edf = 2.68, F = 13.25, P < 0.001), with a stronger increase in selection ratios with increasing values of spatial SD (Figure 4d, same results with residuals SD, Supplementary Appendix 3). Lack of selection for the lowest values of spatial SD, and high values of selection when spatial SD is high, were expected under (H3).

Marginal R^2 were 0.31 and 0.20, respectively for the cluster and the spatial SD variables, while the conditional R^2 were 0.48 and 0.72, meaning that both cluster and spatial SD had strong explicative power.

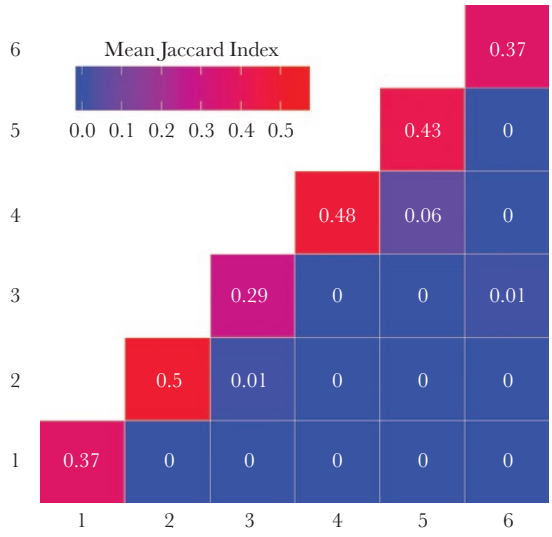

Figure 2
Cluster matrix of Mean Jaccard Index between monthly home range of female chamois.

DISCUSSION

Chamois lived in clusters in which abundance of edible food resources and how these resources were distributed in space differed markedly. Furthermore, annual and month variation in climatic conditions also led chamois to experience different food abundance during the growing season from one year to another. These differences among clusters, months and years in resource abundance and its spatial variation elicited differences in terms of individual habitat selection. However, we unveiled a functional response in selection only vis-à-vis the spatial variation of edible biomass (SD), while surprisingly, chamois did not become less selective when their available range contained more edible biomass. We discuss below these combined patterns of functional response to mean and spatial variation of edible biomass available to individuals.

Functional response and spatial variation of resources

Studying functional response in habitat selection requires the definition of a reference habitat or habitat variable (Johnson 1980) for which 1) availability varies among individual ranges, 2) profitability (related to energy intake or safety) depends on availability (Charnov 1976; Mysterud and Ims 1998). In such cases, availability of this habitat should elicit a response in terms of selection (Van Moorter et al. 2013), which should show up in the form of a functional response in habitat selection. Most often, the food resources available and safety provided by a habitat are described using data on relative proportion of cover types (e.g., habitat categories such as open or closed; Herfindal et al. 2009; land cover types such as grasslands or forests; Bjørneraas et al. 2012). In such cases, spatial variation directly relates to this proportion, being low when the proportion is close to 0 and 1, and high around intermediate values. Hence, the availability of a habitat, and the expected spatial variation of this habitat, are intrinsically correlated. It is more challenging to explore functional responses in habitat selection with regard to continuous measurement of food resources. First, these measures are rarely available in a study site at the individual level (but see e.g., Bastille-Rousseau et al. 2015), as required when looking for functional responses. One can use remote sensing (e.g., Hansen et al. 2009), but only under the assumption of a strong correlation

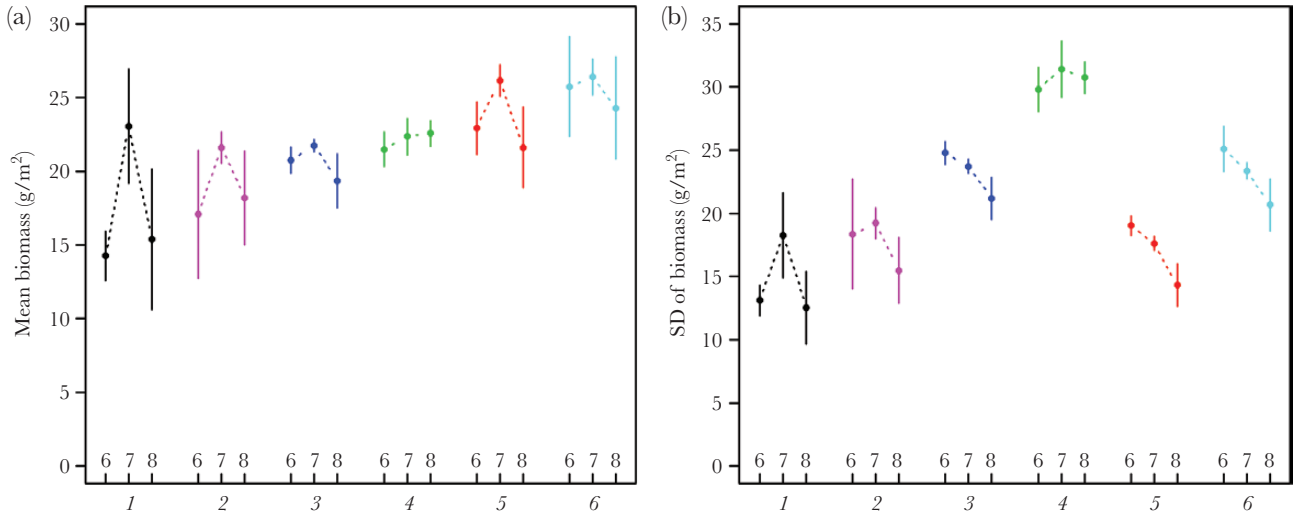

Figure 3
Observed mean and se for the mean (a) and standard deviation (SD; b) of biomass of edible plants (foodscape) by chamois per cluster and month (6: June, 7: July, 8: August). Colors represent clusters (1 to 6; see Figure 1).

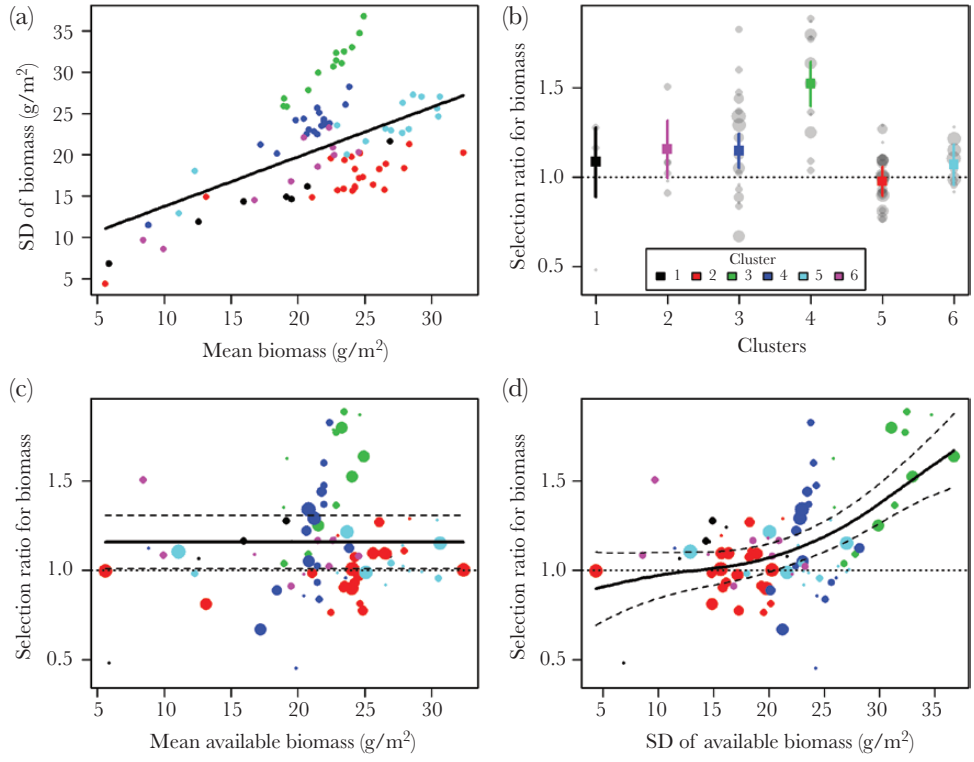

Figure 4
Relationship between mean and SD of edible biomass in each cluster-month-year. Line represents fitted value of a linear regression (a) Individual monthly selection ratios for edible biomass of chamois against 3 variables: clusters mean and 95% CI (b); available mean (c) and SD (d) of edible biomass in each cluster-month-year. Solid and dashed lines represent, respectively, fitted values and 95% CI of the general additive mixed-effect models (n = 212). For the visual representation, selection ratios of individuals were binned by cluster-month-year. Colors represent clusters (see Figure 1) and the size of points (b,c,d) is proportional to sample size (from 1 to 6 individuals by month and year).

between remotely sensed proxies and edible resources, an assumption which can be challenging for small species with a specialized diet (Pettorelli et al. 2005). Second, as we demonstrated here, when the availability of a resource is estimated with continuous variable, there is a need to get an additional measure of the spatial variation in the distribution of the resource (unlike when proportions are used): whatever the mean biomass (whether low or high), animal cannot perform any selection if the biomass is evenly distributed. Yet, while metrics of landscape heterogeneity and of spatial variation of risks are included in movement and habitat selection studies (e.g., Boyce et al. 2003; Morellet et al. 2011; Basille et al. 2015), how the spatial distribution of a resource, controlling for its abundance,

limits or favors selection at the individual level is seldom explicitly studied. Our results unveil such an effect as the spatial variation of edible biomass in available ranges significantly contributed to individual selection, even when controlling for the mean biomass in the available range. It was more surprising to find no effect of the mean available edible biomass on selection, whatever the spatial variation, as we expected individuals to be less selective when resources were abundant. We can relate this lack of saturation effect (Holling 1959; Mezzalira et al. 2017) to the need for this capital breeder species (Jönsson 1997) living in mountains to accumulate fat reserve quickly and ensure the high-energy requirements linked to lactation (Richard et al. 2017) during a short growing season. In addition, for a species with a relatively specialized diet (Bison et al. 2015), biomass of edible plants may never reach too high values, so that moving to areas with more abundant resources may always pay off. We suggest that characterizing spatial variation in resource availability, in addition to mean value, is pivotal for a better understanding variation of individual selection patterns (Gillies et al. 2006; Matthiopoulos et al. 2011).

Measuring functional response to the actual food resources

For relatively small ungulates, such as chamois, with limited ability to digest fibers (Clauss et al. 2003), only a low percentage of the biomass is edible (less than 50% of plant species, Rayé et al. 2011; Bison 2015, which represent about 17% of the total available biomass for chamois, Duparc 2016, unpublished data). It therefore appears crucial to correctly define the food resources available (see Bastille-Rousseau et al. 2015 for a similar approach of assessing resource availability including only plants found in caribou feces) when studying the functional response, given that majority of the biomass in the landscape is not consumed by chamois. Describing the spatio-temporal variability of edible plants only (e.g., the foodscape, Searle et al. 2007) contribute to better assessing the "accessible" component (from the diet point of view) of available resources. While we did not focus here on other drivers of an animal habitat selection, such as risk or heat avoidance (Ruckstuhl and Neuhaus 2002; Marchand et al. 2015; e.g., Bourgoin et al. 2018), the role of resources to determine females habitat selection was detectable, even when most females had a kid at heel and should be incited to use safe areas (Ruckstuhl and Ingold 1999; Ruckstuhl and Neuhaus 2002).

Functional response in habitat selection in group-living species

Functional response in habitat selection was first studied in solitary, territorial, or weakly social species such as roe deer and moose (e.g., Mysterud and Ims 1998; Dussault et al. 2005), where individual ranges hardly overlap. In social species, such as chamois (Crampe et al. 2007; Loison et al. 2008), several individuals can share the same available range. In such cases, functional response in habitat selection needs to account for socio-spatial structures (Hebblewhite and Merrill 2008; Marchand et al. 2015), and for possible correlation in interindividual movements (Torney et al. 2018). While we ignored the latter, since chamois form relatively labile group at the short time scale (Boschi and Nievergelt 2003) and because few of our marked individuals lived in the same cluster the same year, we found marked cluster effects showing that individuals experiencing similar habitat characteristics and resource conditions, responded similarly to cluster range characteristics. Identifying such spatial structure permits a more realistic delimitation of the accessible available range (Panzacchi et al. 2016), under the assumption that the union of the range of individuals that often overlap at the scale of one summer is accessible and know for every individual of the same cluster. This assumption is reasonable given the longevity of this species (Péron et al. 2016). While Beyer et al. (2010) suggest using movement patterns as a way to grasp accessibility (e.g., Bastille-Rousseau et al. 2015 for the application of such an approach), we provide here an alternative solution, grounded in the behavior and life history of our study species (longevive and living in loose groups).

Social interactions participate to the emergence of home ranges (Kaufmann 1983; Powell 2000) and influence movement and habitat selection behavior (e.g., in bison, *Bison bison*, Fortin et al. 2009, in caribou, Torney et al. 2018). Chamois clusters consistently differed in edible biomass, and this raises the question of whether individuals of this group-living species therefore distribute freely according to resource availability (Fretwell and Lucas 1969; Rosenzweig 1981; Morris 1988) at the scale of the population. Chamois being a sedentary species, the vast majority of females keep to their mother's cluster (Loison et al. 2008). Hence, we can expect instead that differences in resource abundance distribution should affect their demographic performance, unless differences in resources are compensated by differences in risk born upon individuals (Basille et al. 2015). To further test the connection between spatial variation in habitat quality, risk, habitat selection, and distribution of animals at the population scale, we need to identify whether or not different individual selection patterns result in spatial differences in individual demographic performances (Gaillard et al. 2010).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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